Allozyme Variation, Genecology, and Phytogeography of Antennaria arcuata (Asteraceae), a Rare Species from the Great Basin and Red Desert with Small Disjunct Populations

Randall J. Bayer

American Journal of Botany, Volume 79, Issue 8 (Aug., 1992), 872-881.

Stable URL:
http://links.jstor.org/sici?sici=0002-9122%28199208%2979%3A8%3C872%3AAVGAPO%3E2.0.CO%3B2-C

American Journal of Botany 79(8): 872–881. 1992.

ALLOZYME VARIATION, GENECOLOGY, AND PHYTOGEOGRAPHY OF ANTENNARIA ARCUATA (ASTERACEAE), A RARE SPECIES FROM THE GREAT BASIN AND RED DESERT WITH SMALL DISJUNCT POPULATIONS[1]

RANDALL J. BAYER

Department of Botany, University of Alberta, Edmonton, Alberta, T6G 2E9

Antennaria arcuata (Asteraceae: Inuleae) is a rare sexual diploid species that occurs in three disjunct regions of Idaho, Nevada, and Wyoming. Isozyme diversity in six populations of the species from the three regions utilized 26 putative loci to provide clues to its population genetic structure. Results show that, in general, the amount of genetic diversity in *A. arcuata* is very low in comparison to other sexual species of *Antennaria*. The values of several genetic statistics such as mean number of alleles per locus, proportion of loci polymorphic, and observed heterozygosity, are significantly lower than populations of any of 17 other sexual species of *Antennaria* that have been studied previously. It is likely that the unusual disjunct and restricted distribution of *A. arcuata* is partially the result of its unusual ecology, as it occurs in moist basins having high concentrations of salts that are frequently disturbed by large grazing animals. Canonical correspondence analysis shows strong relationships between several edaphic, environmental, and geographic features and the genetic variation in the populations. The migration of *A. arcuata* to other regions since the end of the Wisconsinan might have been inhibited by the fact that suitable habitats occur as small isolated islands in a sea of inhospitable terrain, the dry sagebrush steppe.

Antennaria arcuata Cronq. (Asteraceae: Inuleae) is a rare species that occurs in three widely disjunct regions in the Great Basin and Red Desert. It is known from one site in Blaine Co., east of Carey, Idaho; four sites in Elko Co. south of Mountain City, Nevada; and about 18 sites southwest of Atlantic City and two sites northwest of Jeffrey City, Fremont Co., Wyoming. Despite continued searching in likely habitats, the species has not been found in interlying or adjacent areas in Utah (Welsh et al., 1987; Leila Schultz, Utah State University, personal communication) or Colorado (Weber, 1987; William Weber, University of Colorado, personal communication). The species occupies moist depressions in sagebrush steppe or shortgrass prairie, but no detailed analysis of the habitat of the species is available. In fact, since its original description (Cronquist, 1950), the species has received little attention.

Antennaria arcuata is easily distinguished from any other species of *Antennaria* by its conspicuously arching, woolly stolons. The elongating stolons possess only reduced leaves along their length, but a well-developed rosette at their tips. In turn, each rosette is short-lived and produces numerous additional stolons. The densely pubescent basal and cauline leaves are both linear. Staminate and pistillate plants are of equal heights. The heads are strongly dimorphic and possess uniformly light-brown-colored phyllaries.

Cronquist (1950) pointed out that the species was distinct morphologically from any *Antennaria* known to him, but he did not speculate on its phylogenetic relationships. In August 1982, Ledyard Stebbins collected living material of the species from two Nevada sites, which were later determined (Bayer, 1984) as diploid ($2n = 28$). *Antennaria arcuata* is amphimictic, inferred from the fact that populations contain approximately equal proportions of staminate and pistillate plants and that apomixis is unknown at the diploid level in *Antennaria* (Bayer and Stebbins, 1987). The species possesses a large number of plesiomorphic characteristics and has been shown to belong to a monophyletic clade containing two other sexual diploid species, *A. argentea* Benth. and *A. luzuloides* Torr. and Gray (Bayer, 1990a). The monophyletic group 'Argenteae' is unified by the synapomorphous characteristic of densely pubescent stolons, but they have retained the plesiomorphous characters of uniformly colored phyllaries and paniculate synflorescences (Bayer, 1990a). *Antennaria luzuloides* and *A. argentea* possess four synapomorphies not shared by *A. arcuata,* making it the least cohesive member of the group (Bayer, 1990a). As a member of the basal group of species in the genus, *A. arcuata* occupies an important phylogenetic position.

The main objective of this study was to expand our knowledge of the biology of this rare and phylogenetically important taxon, partly in preparation for our taxonomic treatment of the genus for the *Flora of North America* (Bayer and Stebbins, unpublished data). Since *Antennaria* is well known for its intraspecific variation in ploidy level (Bayer and Stebbins, 1987), additional chromosome counts were needed to establish firmly the ploidy level of the species. A phytogeographic history of *A. arcuata* will be advanced through the assistance of a descriptive analysis of the habitat of the species. This may provide clues to the unusual disjunct distribution of its populations. The

[1] Received for publication 21 October 1991; revision accepted 18 March 1992.

The author thanks Travis Minish and Brett Purdy for assistance in the field; Ron Hartman for providing additional locality information for *A. arcuata* in Wyoming; Dan Heaney and the Soils and Animal Nutrition Lab of Alberta Agriculture for providing the selenium analysis of the *Antennaria* plants; Steve Zoltai and Martin Siltanen of the Northern Alberta Forestry Center for providing an analysis of the soil samples; and Jeff Karron and Brett Purdy for helpful comments on the manuscript. This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC grant A3797) and by a University of Alberta Central Research Fund Grant (No. 55-48947).

TABLE 1. *Locality data for six populations of* Antennaria arcuata. *Collectors are R. J. Bayer, T. M. Minish, and B. G. Purdy. Voucher specimens are at ALTA*

State, County	Twp.; Range; Section	Elevation (m above sea level)	Collection number
ID, Blaine Co.	T1S; R22E; Sec. 1/2	1,510	ID-90006
NV, Elko Co.	T45N; R55E; Sec. 29	1,975	NV-90005
WY, Fremont Co.	T31N; R92W; Sec. 17	2,190	WY-90010
WY, Fremont Co.	T28N; R99W; Sec. 5	2,240	WY-90015
WY, Fremont Co.	T28N; R98W; Sec. 24	2,240	WY-90020
WY, Fremont Co.	T29N; R98W; Sec. 26	2,270	WY-90022

population genetic structure and breeding system of the species was assessed using isozymes. Additionally, this study will provide more data on the genetic diversity in geographically restricted rare species, which have been the topic of a recent review (Karron, 1987).

MATERIALS AND METHODS

Field studies—Populations of *A. arcuata* were located using herbarium records from the New York Botanical Garden (NY) and Rocky Mountain Herbarium (RM), and from Marriott (1986). The one Idaho site was relocated, and six Wyoming sites but only one Nevada site was located. Eight collections were relocated, but only six could be used in all aspects of this study (Table 1). Collection numbers are used throughout the text to refer to the sites/populations and are listed in Table 1. In some of the tables and figures collection numbers are abbreviated as follows: 06 = ID-90006; 05 = NV-90005; 10 = WY-90010; 15 = WY-90015; 20 = WY-90020; 22 = WY-90022. At each site soil samples were taken, as well as specimens made of all community associates. For the isozyme variation study, ramets were removed from up to 50 individual *A. arcuata* plants per population. Several meters separated consecutive plants sampled in populations to ensure that different individuals were being sampled. Ramets were transported to the phytotron of the University of Alberta for cultivation and subsequent analysis.

Population genetics and cytology—Chromosome numbers were obtained for the populations using techniques outlined previously (Bayer, 1984; Bayer and Stebbins, 1987). Electrophoretic methodologies are similar to those used previously in *Antennaria* (Bayer, 1988) with some modifications to the extraction buffer (Bayer, 1991). Fresh pieces of actively growing leaf tissue from up to 35 individuals per population were assayed. Tissue was ground in ice-cold extraction buffer, the extract soaked onto filter paper wicks, stored at −20.0 C overnight, and electrophoresed the next morning. Samples were electrophoresed on two 12.0% starch gels. Glutamate dehydrogenase (GDH), glutamate oxaloacetate transaminase (GOT), leucine aminopeptidase (LAP), menadione reductase (MDR), phosphoglucoisomerase (PGI), superoxide dismutase (SOD), and triose-phosphate isomerase (TPI) were resolved on buffer system seven of Soltis et al. (1983). Acid phosphatase (ACP), malate dehydrogenase ((NAD) MDH), phosphoglucomutase (PGM), and shikimic acid dehydrogenase (SKD) were visualized on the histidine (free base)-0.007 M citric acid H_2O (pH 6.5) system of Cardy, Stuber, and Goodman (1981). Enzymatic assays followed Soltis et al. (1983), except for MDR and SOD which followed Wendel and Weeden (1989). The locus specifying the most anodally migrating isozyme was designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a given gene was labeled A, etc.

Genetic variation was described by mean number of alleles per locus (A) (including monomorphic loci), proportion of loci polymorphic (P), observed and expected mean heterozygosities (H_{obs} and H_{exp}, respectively), and mean fixation index (F_T). The observed and expected mean heterozygosities were compared with chi-square tests to determine if the natural populations deviated from Hardy-Weinberg equilibrium expectations. The values for *A. arcuata* for the various genetic statistics were compared to those published values for other species of *Antennaria* using t-tests or Mann-Whitney U-tests (Norusis, 1988). Gene diversity statistics and standard genetic distances and identities were calculated utilizing the methods of Nei (1972, 1973) implemented by the GENESTAT-PC program (Version 2.1, by Paul Lewis and Richard Whitkus; Whitkus, 1988). A matrix of genetic identities was used to generate a minimum spanning tree of the *A. arcuata* populations and was executed using NTSYS-pc (Rohlf, 1987).

Ecology—A genecological study was carried out to compare the similarity of the habitats of these populations with patterns of genetic variation. The analysis used both environmental and community associates data, and the methods were essentially the same as those outlined in an earlier study (Bayer, Purdy, and Lebedyk, in press). Additionally, herbarium specimens of all community associates were collected and identified from each site. The total number of taxa at each site (NTAX) and percent vegetational cover (COVER) were also determined. At each study site elevation (meters) and slope (degrees) were measured using a calibrated barometer and clinometer, respectively. Soil temperature difference (C) between the surface and 10 cm depth, and soil unconfined strength (kg/cm^2), measured by a soil penetrometer, were also recorded.

Soil samples were collected from each of the six study sites, allowed to air dry, and subjected to chemical analysis by the soil analysis laboratory at the Northern Alberta Forestry Center, Edmonton. The nutrients measured include extractable forms of arsenic (As), calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (PO_4), potassium (K), sodium (Na), sulfur (SO_4), and zinc (Zn) measured in parts per million. Total nitrogen was determined and is expressed in percent. The percent organic matter, cation exchange capacity, and pH of the soil were also determined. Selenium content of dried specimens of *A. arcuata* was determined for plants from each population by the Soils and Animal Nutrition Lab of Alberta Agriculture.

Ordination of nominal species data and environmental variables from six study sites was carried out using the canonical correspondence analysis (CCA) option of the Canonical Community Ordination (CANOCO) program (ter Braak, 1985). This method of analysis allows the environmental variables to be related to species data simultaneously and is becoming the preferred ordination

TABLE 2. *Genetic variation in six populations of* Antennaria arcuata *from Idaho, Nevada, and Wyoming*[a]

Population designations (NTAX)	*A*	*P*	$H_{(obs)}$	$H_{(exp)}$	F_T
ID-90006 (12)	1.13 ± 0.338	0.13	0.033	0.046	0.288
NV-90005 (16)	1.13 ± 0.338	0.13	0.053	0.048	−0.106
WY-90010 (13)	1.13 ± 0.342	0.06	0.007	0.007	−0.057
WY-90015 (23)	1.00 ± 0.000	0.00	0.000	0.000	—
WY-90020 (11)	1.16 ± 0.374	0.16	0.076	0.059	−0.279
WY-90022 (11)	1.10 ± 0.301	0.10	0.024	0.034	0.297
Means (±SD)	1.11 ± 0.055	0.10 (±0.06)	0.032 (±0.029)	0.032 (±0.024)	0.029 (±0.25)

[a] Included are: mean number of alleles per locus (*A*); proportion of polymorphic loci, with the most common allele's frequency less than 0.99 (*P*); observed mean heterozygosity ($H_{(obs)}$); expected mean heterozygosity ($H_{(exp)}$); and mean fixation index (F_T). Values of $H_{(obs)}$ and $H_{(exp)}$ are not significantly different at the 1% level. Number of taxa (NTAX) found at each site is provided along with population designations.

method for the analysis of data used in vegetation classification (ter Braak, 1986, 1987, 1988; John, 1989; Gignac and Vitt, 1990; Bayer, Purdy, and Lebedyk, in press). In this study, the ordination was performed to determine and visualize the habitat and species associates of *Antennaria* and to see which environmental variables and species associates best distinguish the study sites from one another. CANOCO was also performed on a second data set that compared the environmental variables with the frequency of alleles at polymorphic loci in each population to determine whether environmental trends existed for the genetic variability. The program was run without any transformation of the variables, weighting environmental variables, or axis rescaling.

RESULTS

Population genetics—The 11 enzyme systems assayed in this study were believed to be coded for by 26 loci. All six populations of *A. arcuata* were determined as diploid ($2n = 28$), and therefore a disomic mode of inheritance for the allozymes can be postulated. The genetic basis of these loci was inferred from segregation patterns observed in *Antennaria* plants from the natural populations. All of the enzyme systems, except MDR, were used previously in isozyme studies of *Antennaria* (Bayer and Crawford, 1986; Bayer, 1988, 1989a, b, 1990b, 1991; Bayer, Ritland, and Purdy, 1990), and details of subcellular localization of isozymes, genetic interpretation, and putative gene duplications in PGI, PGM, and TPI can be found in those publications. The 26 putative isozymes and their allozymes (in parentheses) are ACP-1-(A), ACP-2-(A and B), ACP-3-(A), GDH-1-(A), GOT-1-(A and B), LAP-1-(A), MDH-1-(A), MDH-2-(A), MDH-3-(A), MDH-4-(A), MDR-1-(A), MDR-2-(A), MDR-3-(A and B), PGI-1-(A), PGI-2-(A and B), PGI-3-(A and B), PGM-1-(A), PGM-2-(A and B), PGM-3-(A), PGM-4-(A), SKD-1-(A), SOD-1-(A), SOD-2-(A), TPI-1-(A), TPI-2-(A), and TPI-3-(A). A table of allelic frequencies is available from the author on request.

Most of the loci were monomorphic in all six populations including *Acp-1, Acp-3, Gdh-1, Lap-1, Mdh-1, Mdh-2, Mdh-3, Mdh-4, Mdr-1, Mdr-2, Pgi-1, Pgm-1, Pgm-3, Pgm-4, Skd-1, Sod-1, Sod-2, Tpi-1, Tpi-2,* and *Tpi-3*. The large percentage of monomorphic loci (77%) among the populations is unusually high for *Antennaria,* and even loci that typically display polymorphism in *Antennaria,* i.e., *Acp-3, Lap-1, Skd-1,* and *Tpi-3,* were monomorphic in *A. arcuata.* The other monomorphic loci were generally monomorphic in other species of *Antennaria* as well.

Polymorphism at *Pgi-2* was encountered for the first time in *Antennaria,* but only in some individuals of WY-90010. Two other polymorphic loci were similar to *Pgi-2* in that rare alternative alleles were in low frequency and in single populations, *Pgi-1*^{a} was found only in WY-90020, and *Got-1*^{b} also in WY-90020. PGI-1-A is an allozyme that has the same electrophoretic mobility as an allozyme (also designated as PGI-1-A), which is monomorphic in another sexual species of *Antennaria, A. microphylla* Rydb. (Bayer, 1988). This species co-occurred with *A. arcuata* on drier adjacent margins of the WY-90020 site (Table 6).

The mean number of alleles per locus (*A*) in *A. arcuata* ranges from 1.00 to 1.16 (mean = 1.11; Table 2). Values for the proportion of loci polymorphic (*P*) range from 0.0 to 0.16 with an interpopulational mean of 0.10 (Table 2). The mean observed heterozygosity ($H_{(obs)}$) has a mean value of 0.032 (range 0.0 to 0.076; Table 2). None of the values for ($H_{(obs)}$) were significantly different from expected values ($H_{(exp)}$) based on the Hardy-Weinberg model (Table 2). The mean fixation index (F_T), a useful measure of the degree of inbreeding, ranges from −0.279 to 0.288 (mean = 0.029) in populations of *A. arcuata.* Complete outcrossing would be expected of a sexual dioecious breeding system (Table 2), but in two populations (ID-90006 and WY-90022) functional inbreeding, i.e., matings among closely related individuals, may be occurring because the values of F_T are above 0.1 (Table 2).

Gene diversity statistics (Table 3) are related by the following sets of equations: Total gene diversity (H_T) = gene diversity within populations (H_S) + gene diversity between populations (D_{ST}). The coefficient of gene diversity, $G_{ST} = D_{ST}/H_T$. Among the six polymorphic loci only three, *Mdr-3, Pgm-2, Acp-2,* had relatively substantial amounts of total gene diversity (Table 3). The mean (H_T) over all six loci is 0.0579 (range 0.010 to 0.4726). The mean value of G_{ST} for *A. arcuata* over all loci is 0.196, indicating that most of the genetic diversity resides within populations (H_S) instead of among populations (D_{ST}), as is typical of outcrossing species.

Table 4 presents a matrix of Nei's genetic identities (*I*) and distances (*D*) for individual population pairwise comparisons and mean intraspecific comparisons. The values

TABLE 3. *Nei's genetic diversity statistics for six populations of* A. arcuata. *Presented are gene diversities for individual polymorphic and pooled loci*[a]

Loci	H_T	H_S	D_{ST}	G_{ST}
Acp-2	0.3165	0.2919	0.0246	0.0777
Got-1	0.2320	0.1627	0.0693	0.2987
Mdr-3	0.4726	0.3313	0.1413	0.2991
Pgi-2	0.0100	0.0099	0.0000	0.0000
Pgi-3	0.0166	0.0162	0.0004	0.0237
Pgm-2	0.4576	0.4054	0.0522	0.1141
All loci	0.0579	0.0468	0.0111	0.1959

[a] Only loci displaying polymorphism are represented; monomorphic loci have gene diversity statistics values of 0.000. H_T = Total gene diversity within a taxon; H_S = gene diversity within populations of a taxon; D_{ST} = gene diversity between populations within a taxon; G_{ST} = coefficient of gene differentiation.

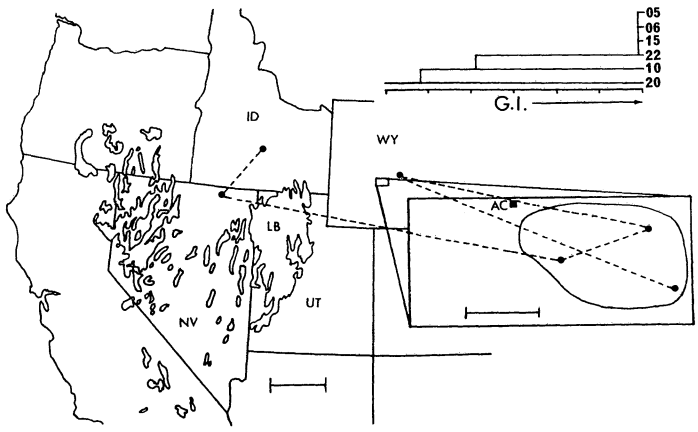

Fig. 1. Geographic positions of six populations used in the ecological and isozymic studies of *Antennaria arcuata* from Idaho (ID), Nevada (NV), and Wyoming (WY). The distribution of numerous Pleistocene Lakes (Meinzer, 1922) is shown, the largest being Lake Bonneville (LB) in western Utah (UT). Inserted is a small scale map of the area southeast of Atlantic City (AC), where *A. arcuata* is most abundant. Solid line within the insert is the outline of the range occupied by about 18 known localities of *A. arcuata* within the area, where three populations were sampled for this study. A minimum spanning tree (upper right) was derived from the matrix of genetic identities (Table 4). Population designations are 06 = ID-90006, 05 = NV-90005, 10 = WY-90010, 15 = WY-90015, 20 = WY-90020, 22 = WY-90022. The minimum spanning tree was superimposed on the map, connecting the populations (dotted line) to illustrate their genetic relationships. Bar on large scale map = 200 km. Bar on insert = 10 km.

of I and D are very high and low, respectively, for interpopulation comparisons (Table 4). The range of values for I is 0.9797 to 1.00 (mean = 0.9944), whereas the range of values for D is 0.00 to 0.0209 (mean = 0.0708). The Nevada and Idaho populations (ID-90006 and NV-90005) are more similar to each other than are several Wyoming populations to each other (Table 4; Fig. 1).

Ecology and genecology—Examination of Table 5 reveals that the soils of the *A. arcuata* sites are of neutral to high pH and also have high amounts of organic matter. They are also very high in several minerals including most notably calcium, magnesium, and sodium. These values are higher than those encountered for nine previously investigated species of *Antennaria,* except for the calciphilous species, *A. aromatica* and the halophilous species, *A. microphylla* (Bayer, Purdy, and Lebedyk, in press). The edaphic composition of the sites of *A. arcuata* are most similar to those of *A. microphylla,* except they are moister. This can be readily seen in the field where the two coexist because *A. microphylla* grows on the dry margins of the moist basins where *A. arcuata* occurs. Chemical analysis of *A. arcuata* confirmed small amounts of selenium, but these values (Table 5) are at the low end of the spectrum of values that are typical of plants growing in soils high in selenium (Rosenfeld and Beath, 1964). However, one of the most common community associates of *A. arcuata, Aster adscendens* (Table 6), is a well-known secondary indicator of selenium soils (Rosenfeld and Beath, 1964).

In the ordination diagrams (Figs. 2, 3), the lines representing environmental variables point in the direction of maximum change in that variable, and the length of the line indicates a relative measure of the rate of the change in that variable (ter Braak, 1987). Therefore, longer lines are more important parameters than short ones and tend to be more closely related to the patterns of community variation (ter Braak, 1987). The relative position of each *Antennaria* species site, community associate, or allele can best be viewed by projecting the points onto the lines. This is accomplished by first extending each line, either on paper or in the mind, in both directions to the edge of the diagram. Then draw or visualize a line from the site symbols, perpendicular to the line until it intersects the line. The ranking of those endpoints along the line is an approximate indication of the relative value of the weighted mean of each species site with respect to that environmental variable. Also, the origin of the line indicates the grand mean; therefore if the endpoint of the line lies on the same side of the origin as the perpendicular intersect, then that site has a weighted mean that is higher than the grand mean and vice-versa in the other direction (ter Braak, 1986).

From Fig. 2 we can deduce that three of the Wyoming populations (WY-90010, WY-90015, and WY-90020) are ecologically quite similar to each other, whereas the other Wyoming site is the most unusual of the Wyoming sites because it has a different set of species associates and has relatively high amounts of selenium in the plants and zinc in the soil. The site is also characterized by relatively low amounts of calcium, copper, iron, and sulfur in the soil, and is of a lower pH than the other sites (Fig. 2). The four Wyoming sites, since they are closer to the center of the

TABLE 4. *Nei's genetic distances (lower triangle) and genetic identities (upper triangle) for all pairwise comparisons of six populations of* Antennaria arcuata. *Mean intraspecific genetic distance and genetic identity for the six populations of* A. arcuata *are 0.9944 and 0.0723, respectively*

Populations	ID-90005	NV-90006	WY-90010	WY-90015	WY-90020	WY-90022
ID-90005	—	0.9967	0.9996	1.0000	0.9793	1.0000
NV-90006	0.0033	—	0.9928	1.0000	0.9804	0.9924
WY-90010	0.0004	0.0073	—	1.0000	0.9857	0.9992
WY-90015	0.0000	0.0000	0.0000	—	0.9996	1.0000
WY-90020	0.0209	0.0198	0.0144	0.0004	—	0.9904
WY-90022	0.0000	0.0077	0.0008	0.0000	0.0097	—

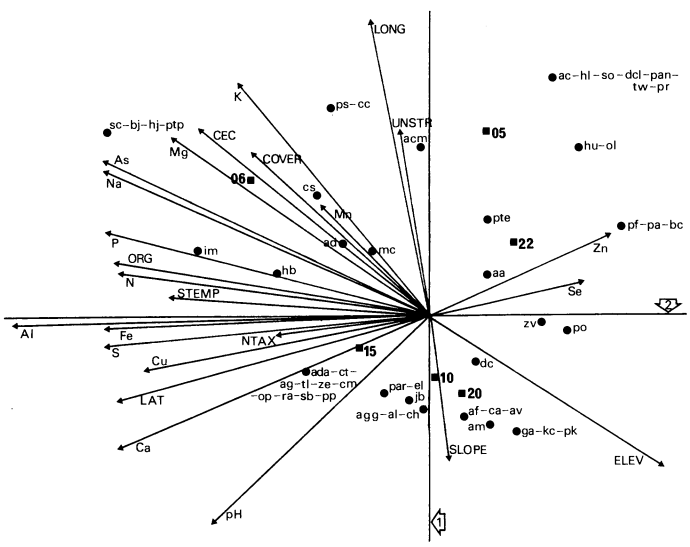

Fig. 2. The distribution of six study sites of *Antennaria arcuata* (solid squares) and community associates (solid circles) along CCA ordination axes 1 and 2 with environmental variables indicated by arrows. See text for guidance in interpretation of this diagram and explanation of methods. Environmental factor abbreviations are as follows: extractable forms of aluminum (Al); arsenic (As); calcium (Ca); copper (Cu); iron (Fe); magnesium (Mg); manganese (Mn); phosphorus (P); potassium (K); sodium (Na); sulfur (S); and zinc (Zn); and percent organic matter (OR); cation exchange capacity (CEC); total soil nitrogen (N); soil temp (STEMP); percent cover (COVER); elevation (ELEV); latitude (LAT); longitude (LONG); selenium in dried plants (Se); slope (SLOPE); pH (pH); number of taxa at each site (NTAX); and soil unconfined strength (UNST). Site abbreviations for *A. arcuata* are 06 = ID-90006, 05 = NV-90005, 10 = WY-90010, 15 = WY-90015, 20 = WY-90020, 22 = WY-90022. Community associates are represented on the ordination axes as lowercase letters, and these abbreviations are explained in Table 6. Several species may be represented by one letter.

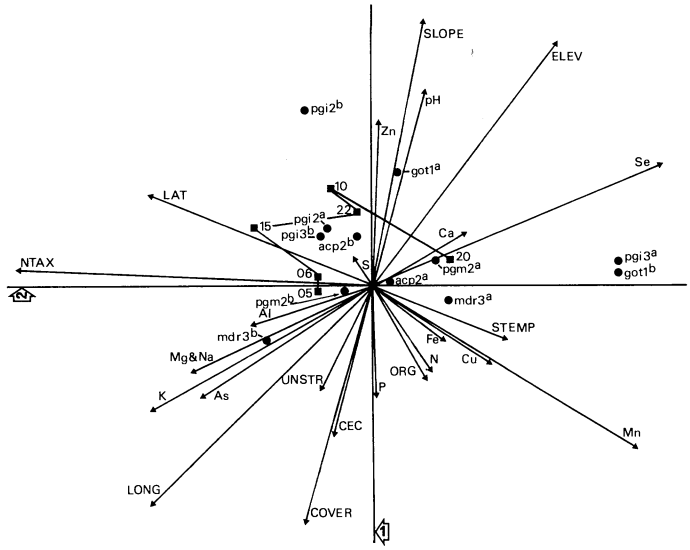

Fig. 3. The distribution of six study sites of *Antennaria arcuata* (solid squares) and alleles at polymorphic loci (solid circles) along CCA ordination axes 1 and 2 with environmental variables indicated by arrows. See text for guidance in interpretation of this diagram and explanation of methods. Environmental factor abbreviations are as follows: extractable forms of aluminum (Al); arsenic (As); calcium (Ca); copper (Cu); iron (Fe); magnesium (Mg); manganese (Mn); phosphorus (P); potassium (K); sodium (Na); sulfur (S); and zinc (Zn); and percent organic matter (OR); cation exchange capacity (CEC); total soil nitrogen (N); soil temp (STEMP); percent cover (COVER); elevation (ELEV); latitude (LAT); longitude (LONG); selenium in dried plants (Se); slope (SLOPE); pH (pH); number of taxa at each site (NTAX); and soil unconfined strength (UNST). Site abbreviations for *A. arcuata* are 06 = ID-90006, 05 = NV-90005, 10 = WY-90010, 15 = WY-90015, 20 = WY-90020, and 22 = WY-90022. The minimum spanning tree was superimposed on the ordination, connecting the populations (solid line) to illustrate their genetic relationships.

TABLE 5. *Soil composition and environmental variables from six sites containing* Antennaria arcuata[a]

Soil/plant components	Sites[b]					
	06	05	10	15	20	22
pH	7.26	6.36	7.75	7.54	7.38	6.78
N (%)	1.3258	0.2138	0.2082	0.6779	0.8532	0.5726
CEC (meq/100 g)	60.792	26.692	15.392	21.592	32.372	32.532
% OR	20.4792	3.6028	2.6169	10.6189	13.4632	9.2915
P	46.44	2.177	5.943	7.430	20.02	3.761
S	219.9	26.93	136.0	97.70	127.6	66.99
Mg	1,653	618.3	674.0	448.7	532.0	733.5
As	0.466	<0.000	<0.000	<0.000	<0.000	<0.000
Na	2,923	130.7	508.1	71.30	89.08	138.7
Al	1.411	<0.000	0.494	0.799	0.506	<0.000
Zn	<0.000	<0.000	<0.000	<0.000	<0.000	30.97
Cu	0.516	0.142	0.073	0.582	0.547	0.216
K	933.1	507.5	406.5	219.3	287.2	400.0
Mn	10.19	6.624	3.640	5.407	10.70	6.538
Fe	2.566	0.167	0.556	1.477	1.860	0.934
Ca	8,200	3,196	6,937	7,158	7,646	4,159
Se	0.08	0.04	0.06	0.03	0.12	0.16
STEMP (C)	16.0	6.0	9.0	8.0	13.0	8.0
UNSTR (kg/cm^2)	4.5	3.75	3.75	2.5	3.5	3.5
SLOPE (degrees)	0.0	0.0	1.0	2.0	1.0	2.0
COVER (percent)	100.0	100.0	90.0	100.0	98.0	95.0

[a] Presented are minerals (in ppm) abbreviations as follows: aluminum (Al); arsenic (As); calcium (Ca); copper (Cu); iron (Fe); magnesium (Mg); manganese (Mn); phosphorus (P); potassium (K); sodium (Na); sulfur (S); and zinc (Zn); and percent organic matter (% OR); cation exchange capacity (CEC); and total soil nitrogen (N); as well as soil temperature difference between the surface and 10 cm depth (STEMP); unconfined soil strength (UNSTR); slope (SLOPE); and percent cover (COVER). Selenium content from plants (Se) is given in ppm on a dry weight basis. Other environmental factors can be found in Table 1.

[b] Site abbreviations: 06 = ID-90006; 05 = NV-90005; 10 = WY-90010; 15 = WY-90015; 20 = WY-90020; 22 = WY-90022.

TABLE 6. *Community associates from six sites containing populations of* Antennaria arcuata[a]

Taxa	Abbreviation	Sites[b]					
		06	05	10	15	20	22
Asteraceae:							
Achillea millefolium L.	acm	+	+	−	−	−	+
Agoseris glauca (Pursh) Raf. var. *glauca*	agg	−	−	+	+	+	−
Agoseris glauca (Pursh) Raf. var. *dasycephala* (Torr. & Gray) Jeps.	ada	−	−	−	+	−	−
Antennaria microphylla Rydb.	am	−	−	+	−	+	−
Artemisia cana Pursh	ac	−	+	−	−	−	−
Aster adscendens Lindl.*	aa	−	+	+	+	−	+
Aster falcatus Lindl.	af	−	−	+	−	−	−
Aster lonchophyllus Hook.	al	−	−	+	+	+	−
Cirsium hookerianum Nutt.	ch	−	−	+	+	+	−
Crepis tectorum L.	ct	−	−	−	+	−	−
Haplopappus lanceolatus (Hook.) Torr. & Gray	hl	−	+	−	−	−	−
Haplopappus uniflorus (Hook.) Torr. & Gray	hu	−	+	−	−	−	+
Senecio canus Hook.	sc	+	−	−	−	−	−
Cyperaceae:							
Carex aurea Fern.	ca	−	−	+	−	−	−
Carex simulata Mack.	cs	+	+	−	+	−	−
Equisetaceae:							
Equisetum laevigatum A. Br.	el	−	−	+	+	−	−
Fabaceae:							
Astragalus gracilis Nutt.	ag	−	−	−	+	−	−
Astragalus vexilliflexus Sheld.	av	−	−	+	−	−	−
Trifolium longipes Nutt. var. *reflexum* A. Nels.	tl	−	−	−	+	−	−
Gentianaceae:							
Gentiana affinis Griseb. var. *affinis*	ga	−	−	−	−	+	−
Iridaceae:							
Iris missouriensis Nutt.	im	+	−	−	+	−	−
Juncaceae:							
Juncus balticus Willd. var. *montanus* Engelm.	jb	−	−	−	+	+	−
Liliaceae:							
Zigadenus elegans Pursh	ze	−	−	−	+	−	−
Zigadenus venenosus Wats. var. *gramineus* (Rydb.) Walsh	zv	−	−	+	−	−	+
Malvaceae:							
Sidalcea oregana (Nutt. ex Torr. & Gray) Gray	so	−	+	−	−	−	−
Poaceae:							
Agropyron dasystachyum (Hook.) Scribn. var. *riparium* (Scribn. & Smith) Bowden	ad	+	−	−	+	−	−
Bromus ciliatus L.	bc	−	−	−	−	−	+
Bromus japonicus Thunb.	bj	+	−	−	−	−	−
Calamagrostis montanensis (Scribn.) Scribn. in Vasey	cm	−	−	−	+	−	−
Danthonia californica Bolander	dcl	−	+	−	−	−	−
Deschampsia cespitosa (L.) Beauv.	dc	−	−	+	+	+	+
Hordeum brachyanthenum Nevski	hb	+	−	+	−	−	−
Hordeum jubatum L.	hj	+	−	−	−	−	−
Koeleria cristata Pers.	kc	−	−	−	−	+	−
Muhlenbergia cuspidata (Torr.) Rydb.	mc	+	+	−	+	+	−
Oryzopsis pungens (Torr. ex Spreng.) Hitchc.	op	−	−	−	+	−	−
Poa annua L.	pan	−	+	−	−	−	−
Poa arida Vasey	par	−	−	+	+	−	−
Poa sandbergii Vasey	ps	+	+	−	−	−	−
Trisetum wolfii Vasey	tw	−	+	−	−	−	−
Polemoniaceae:							
Phlox kelseyi Britton	pk	−	−	−	−	+	−
Ranunculaceae:							
Ranunculus acriformis Gray var. *acriformis*	ra	−	−	−	+	−	−

TABLE 6. *Continued*

Taxa	Abbreviation	Sites[b] 06	05	10	15	20	22
Rosaceae:							
Pentaphylloides floribunda (Pursh) Löve	pf	−	−	−	−	−	+
Potentilla gracilis Dougl. ex Hook. var. *elmeri* (Rydb.) Jeps.	pte	−	+	−	+	−	+
Potentilla gracilis Dougl. ex Hook. var. *pulcherrima* (Lehm.) Fern.	ptp	+	−	−	−	−	−
Potentilla anserina L.	pa	−	−	−	−	−	+
Potentilla ovina Macoun var. *ovina*	po	−	−	−	−	+	+
Salicaceae:							
Salix geyeriana Anderss.	sb	−	−	−	+	−	−
Saxifragaceae:							
Parnassia palustris L. var. *montanensis* (Fern. & Rydb. ex Rydb.) Hitchc.	pp	−	−	−	+	−	−
Scrophulariaceae:							
Castilleja cusickii Greenm.	cc	+	+	−	−	−	−
Orthocarpus luteus Nutt.	ol	−	+	−	−	−	+
Penstemon rydbergii A. Nels. var. *oreocharis* (Greene) Holmgren	pr	−	+	−	−	−	−
Total number of taxa per site (NTAX)—		12	16	13	23	11	11

[a] Presented are taxon names arranged alphabetically by family and occurrence (+ = present; − = absent) at each of the sites listed in Table 1. * = known selenium indicator/accumulator species. Abbreviations refer to those abbreviations used in Fig. 2 to represent the taxa. Total number of taxa/site is also given.

[b] Site abbreviations: 06 = ID-90006; 05 = NV-90005; 10 = WY-90010; 15 = WY-90015; 20 = WY-90020; 22 = WY-90022.

diagram, are the more ecologically typical of the six sites, whereas the Idaho and Nevada sites are more atypical, being at the margins of the diagram. The Idaho site differs from the Nevada and Wyoming sites with respect to a number of environmental factors such as higher amounts of manganese, potassium, magnesium, arsenic, sodium, and phosphorus in the soil, as well as more highly compacted soils with higher organic matter and cation exchange capacity (Fig. 2). This site also had a higher percent vegetation cover than the Wyoming sites (Fig. 2). The typical community associates of *A. arcuata* are those taxa that are usually nearest to the center of the ordination (Fig. 2) and include species such as *Deschampsia cespitosa, Aster adscendens* (a selenium indicator species), *Muhlenbergia cuspidata, Potentilla gracilis* var. *elmeri, Agoseris glauca* var. *glauca, Aster lonchophyllus, Cirsium hookerianum, Carex simulata,* and *Achillea millefolium,* and less often *Agropyron dasystachyum* var. *riparium, Equisetum laevigatum, Antennaria microphylla, Zigadenus venenosus* var. *gramineus, Juncus balticus* var. *montanus, Poa arida, Potentilla ovina* var. *ovina, Castilleja cusickii,* and *Orthocarpus luteus* (Table 6). Each site has several species that are unique to that particular site (Fig. 2; Table 6).

The genetic relationships among the sites with regard to the environmental factors can be seen in Fig. 3. Alleles that show the strongest relationships with environmental and geographic features include *Pgi-3*^{a}, *Got-1*^{a}, *Got-1*^{b}, *Pgi-2*^{b}, and *Mdr-3*^{b} (Fig. 3). *Pgi-3*^{a} and *Got-1*^{b}, found only at WY-90020, were associated with relatively high amounts of selenium in the plants, high manganese in the soil, low amounts of sodium, potassium, and magnesium, and low taxonomic diversity (NTAX) of community associates (Fig. 3). However, associations between environmental characteristics and rare alleles that occur in only one population must be considered with caution. High frequency of the alternative alleles to the rare alleles, *Pgi-3*^{b} and *Got-1*^{a}, tend to be associated with the opposite environmental conditions, although both alleles at *Got-1* are associated with soils that are high in pH and zinc as well as sites that are at the highest elevations (Fig. 3). The frequencies of *Mdr-3*^{a} and *Mdr-3*^{b} also display strong environmental and geographic trends; *Mdr-3*^{b} is found only in the westernmost populations (ID-90006 and NV-90005) at low elevations and is associated with high amounts of arsenic, magnesium, potassium, and sodium in the soil, relatively low amounts of selenium in the plants, at sites with a high percent cover and high taxonomic diversity among the community associates (Fig. 3). *Mdr-3*^{a} displays the opposite trends with respect to these factors (Fig. 3). *Pgi-2*^{b} occurs only in plants at population WY-90010, which is the easternmost Wyoming population and is geographically isolated from the main Wyoming populations southeast of Atlantic City. This site is characterized by soil that has a low cation exchange capacity and is high in pH, but relatively low in organic matter, manganese, nitrogen, iron, and phosphorus (Fig. 3). *Pgm-2* and *Acp-2* are examples of loci whose alleles show only weak connection with environmental factors (Fig. 3). Overall the minimum spanning tree again reinforces the strong genetic and edaphic similarity between the two western sites from Idaho and Nevada and their similarity to the Wyoming site (WY-90015) (Fig. 3). WY-90020 is the most edaphically and genetically distinct population, whereas WY-90010 and WY-90022 are most similar (Fig. 3).

TABLE 7. *Table of the genetic statistics A, P, $H_{(OBS)}$, F_T, H_T, and G_{ST} for various groups of* Antennaria *for comparison to* A. arcuata[a]

Genetics statistic-(test used) and group for comparison	Values of genetic statistics for various groups		
	Endemics	Endemics + Other	Other
A-(T)			
A. arcuata	1.30*	1.31*	—
A-(T)			
A. arcuata + endemics	—	—	1.31
P-(T)			
A. arcuata	0.230*	0.226*	—
P-(T)			
A. arcuata + endemics	—	—	0.228
$H_{(OBS)}$-(T)			
A. arcuata	0.088*	0.093*	—
$H_{(OBS)}$-(T)			
A. arcuata + endemics	—	—	0.094
F_T-(T)			
A. arcuata	−0.110	−0.360	—
F_T-(T)			
A. arcuata + endemics	—	—	−0.371
H_T-(U)			
A. arcuata	0.102	0.109	—
H_T-(U)			
A. arcuata + endemics	—	—	0.093
G_{ST}-(U)			
A. arcuata	0.077	0.132	—
G_{ST}-(U)			
A. arcuata + endemics	—	—	0.150

[a] Groups were compared by *t*-tests (T) or Mann-Whitney *U*-tests (U). Genetic statistics for *A. arcuata* are given in Table 2. "Endemic" species are geographically restricted endemics other than *A. arcuata* and include *A. aromatica, A. densifolia, A. pulchella,* and *A. virginica.* "Other" species are *A. corymbosa, A. friesiana* ssp. *alaskana, A. marginata, A. media, A. microphylla, A. monocephala* ssp. *monocephala, A. neglecta, A. neoalaskana, A. plantaginifolia, A. racemosa, A. rosulata, A. solitaria,* and *A. umbrinella.* * = significantly different at 5% level.

DISCUSSION

Population genetics—A considerable amount of data exists concerning the population genetics of *Antennaria* (Bayer and Crawford, 1986; Bayer, 1988, 1989a, b, 1990b, 1991; Bayer, Ritland, and Purdy, 1990), but *A. arcuata* will be compared only to other sexual species of *Antennaria* (data from Bayer and Crawford, 1986; Bayer, 1988, 1989b, 1991). Comparisons will also be made between *A. arcuata* and a group of four other narrowly restricted endemic species of *Antennaria, A. aromatica* Evert, *A. densifolia* Porsild, *A. pulchella* Greene, and *A. virginica* Stebbins. In general, the amounts of genetic diversity in *A. arcuata* are low in comparison to other sexual species of *Antennaria* (Table 7). The values of *A, P,* and $H_{(OBS)}$ are significantly lower than populations of any of 17 other sexual species of *Antennaria* (138 populations) that have been studied (Table 7). The four other endemic species of *Antennaria* (22 populations) also have significantly higher values for *A, P,* and $H_{(OBS)}$ than the six populations of *A. arcuata* (Table 7).

The fixation indices (F_T) for *A. arcuata* are somewhat higher than most other populations of *Antennaria.* The values of F_T for *A. arcuata* and the group of other endemics approach statistical difference ($P = 0.1$) from those for widespread sexual species (Table 7), although since these values vary considerably within *A. arcuata* and the other endemics, a comparison to its congeners must be considered with caution. Nonetheless, this may indicate that smaller population sizes and geographic isolation in some populations of these endemics may engender more functional inbreeding through the crossing of closely related individuals within these populations. The values for G_{ST} for *A. arcuata* and the other endemics are lower (although not of statistical significance) than those for the other widespread species (Table 7), and this means that genetic diversity in the endemics tends to reside more within populations (H_S) than among populations (D_{ST}). This result may indicate that gene flow among populations of the endemics still occurs. Additionally, since PGI-1-A was found only in *A. arcuata* at WY-90020 and is an allozyme that has the same electrophoretic mobility as an allozyme that is monomorphic in *A. microphylla,* introgression may be occurring between *A. arcuata* and *A. microphylla,* which co-occur at the WY-90020 site (Table 6).

In a recent review of levels of genetic diversity among geographically widespread and restricted congeners, Karron (1987) noted that past evolutionary dogma concerning geographically restricted endemics with small population sizes state that such populations should contain less genetic diversity than their widespread congeners. Karron's review (1987) found that overall, some endemics did have much lower levels of genetic polymorphism than did their widespread relatives, but in some groups the endemics had just as much genetic diversity as their widespread congeners. Many additional studies after this review (Karron, 1987) have continued to find that geographically restricted endemics have less genetic diversity than their widespread relatives (Karron et al., 1988; Moran, Muona, and Bell, 1989; Pleasants and Wendel, 1989; Van Treuren et al., 1991), although some have also found relatively high amounts of diversity in some endemics (Coates, 1988; Nickrent and Wiens, 1989; Kuittinen et al., 1991). *Antennaria arcuata* definitely has lower amounts of genetic diversity than its widespread congeners, but it also has lesser amounts than other geographically restricted species of *Antennaria.* Its genetic statistics, *A* and *P,* are also lower than most of those cited by Karron (1987) in his summary of geographically restricted species.

Ecology, genecology, and phytogeographic history—The unusual disjunct and restricted distribution of *A. arcuata* is partially the result of its peculiar ecology. It occurs in the centers of moist basins that are surrounded by sagebrush steppe, where it is regularly affiliated with a fairly large number of typical community associates (Table 6; Fig. 2). Soil analysis indicates that high salt deposits on the soil surface in these areas undoubtedly leach from adjacent areas. These basins suffer disturbance from domestic animals, primarily range cattle, which are attracted by moisture and the relatively lush vegetation. These same areas were perhaps also disturbed by plains bison during precolonial times. *Antennaria arcuata* occurs on the sides of hummocks that are created by cattle activity in the moist sloughs. Halophytic plants generally grow in areas whose soils have salt concentrations of greater than 100 mM (Flowers, Hajibagheri, and Clipson, 1986). The mean

concentration of sodium in the soils of the sites was 27.0 mM, and, although one site (ID-90006) had a sodium concentration of 127.0 mM, the remaining sites must be considered as marginally halophytic. Preference for seleniferous soils might be another factor limiting the distribution of the species, as the *A. arcuata* plants from some sites did have small amounts of selenium in their aboveground parts (Table 5), were associated with a known selenium indicator plant, *Aster adscendens* (Table 6), and were found in regions that have large amounts of seleniferous soils (Rosenfeld and Beath, 1964).

The genecological portion of this study investigated the distribution and ecological significance of the genetic variation in populations of *A. arcuata.* Much controversy still exists regarding whether ecological selection, stochastic processes, and/or the neutrality of allozyme variation is the fundamental cause of allozymic differentiation in plant populations (Nevo, Beiles, and Krugman, 1988b). A large number of studies are now beginning to demonstrate that ecological selection does act on specific allozyme loci (reviewed in Nevo, Beiles, and Krugman, 1988b) or blocks of genes linked to these loci (Nevo, Beiles, and Krugman, 1988a). Results from this study indicate that ecological factors, especially edaphic ones, may be exerting selective pressures on several of the allozymes, including *Pgi-3^a, Got-1^a, Got-1^b, Pgi-2^b,* and *Mdr-3^b,* or gene complexes linked to them. However, correlation between environmental characteristics and rare alleles that occur in only one population, such as *Pgi-2^b, Pgi-3^a,* and *Got-1^b,* must be viewed with caution. Nonetheless, this could lead to continued micro- and macrogeographic differentiation among the populations of *A. arcuata.* If gene flow among these small, isolated populations is minimal, this will tend to reinforce differentiation at the population level, especially between the eastern (Wyoming) and western (Idaho and Nevada) populations. Additionally, theoretical models, in accordance with the niche-width variation hypothesis (Van Valen, 1965), predict that more allozyme diversity should be encountered in the more heterogeneous environments. If we agree that community associate diversity (i.e., number of taxa per site [NTAX]) is a genuine indicator of niche-width (Harper, 1977), a comparison of some indicators of genetic diversity with NTAX (Table 6) shows a trend that is the opposite of what might be expected. The most edaphically variable site (WY-90015) has the lowest amounts of allozyme diversity (Table 2), whereas the least variable sites have higher amounts of diversity.

Antennaria arcuata was once more widely distributed. The presently existing sites could be the remnants of populations that represented the margin of the range of the species. Increased moisture during the Pleistocene led to heavy snows in the Wasatch and other mountain ranges of the Great Basin (Antevs, 1952). This ultimately led to the formation of large inland lakes in the Basin including Bonneville (water level about 277 m above the Great Salt Lake), Lahontan, and about 66 other smaller lakes (Fig. 1; Meinzer, 1922; Smith, 1978). Populations of *A. arcuata* that may have existed in the central portion of its former range were likely extirpated by glacial lakes, and current populations are the remnants of those that existed along the margin of the distribution of this taxon (Fig. 1).

The mean annual temperature in the Great Basin area was estimated to be only 2.5–3 C lower than the current mean annual temperature in the region (Antevs, 1952) and 10–15 C lower in the Rockies (Porter, Pierce, and Hamilton, 1989). Glaciation was restricted to the mountains and was most extensive in the Salmon River Ranges, Uinta Mountains, and Wind River Range, and less extensive in the Wasatch Ranges and Mountains of Nevada (Richmond, 1986; Porter, Pierce, and Hamilton, 1989). The valleys of the Great Basin were most likely a mosaic of coniferous forest, steppe, and meadow, much as they are today, except islands of coniferous forest vegetation were larger during the Wisconsinan (Thompson and Mead, 1982). It is probable that many plant species, possibly including *A. arcuata,* in the Great Basin persisted in situ and did not migrate to any great extent during the Wisconsinan in response to climatic change (McLaughlin, 1986; Thompson, 1988). Genetic identities (*I*) support this phytogeographic scenario because they point to the geographic differentiation among the six populations from the three geographic regions, suggesting their relatively long isolation. The migration of the genetically depauperate *A. arcuata* to other regions since the end of the Wisconsinan might have been reduced because suitable habitats occurred only as small isolated islands in the dry sagebrush steppe following the hypsithermal.

LITERATURE CITED

ANTEVS, E. 1952. Cenozoic climates of the Great Basin. *Geologische Rundschau* 40: 94–108.

BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). *Systematic Botany* 9: 74–83.

———. 1988. Patterns of isozyme variation in western North American *Antennaria* (Asteraceae: Inuleae). I. Sexual species of section *Dioicae. Systematic Botany* 13: 525–537.

———. 1989a. Patterns of isozyme variation in the *Antennaria rosea* (Asteraceae: Inuleae) polyploid agamic complex. *Systematic Botany* 14: 389–397.

———. 1989b. Patterns of isozyme variation in western North American *Antennaria* (Asteraceae: Inuleae). I. Diploid and polyploid species of section *Alpinae. American Journal of Botany* 76: 679–691.

———. 1990a. A phylogenetic reconstruction of *Antennaria* Gaertner (Asteraceae: Inuleae). *Canadian Journal of Botany* 68: 1389–1397.

———. 1990b. Patterns of clonal diversity in the *Antennaria rosea* (Asteraceae) polyploid agamic complex. *American Journal of Botany* 77: 1313–1319.

———. 1991. Isozymic and morphological variation in low arctic species of *Antennaria* (Asteraceae: Inuleae) from northwestern North America. *Systematic Botany* 16: 492–506.

———, AND D. J. CRAWFORD. 1986. Allozyme divergence among five diploid species of *Antennaria* (Asteraceae: Inuleae) and their allopolyploid derivatives. *American Journal of Botany* 73: 287–296.

———, B. G. PURDY, AND D. G. LEBEDYK. In press. Niche differentiation among eight sexual species of *Antennaria* Gaertner (Asteraceae: Inuleae) and *A. rosea,* their allopolyploid derivative. *Evolutionary Trends in Plants* 5: 109–123.

———, K. RITLAND, AND B. G. PURDY. 1990. Evidence of partial apomixis in *Antennaria media* (Asteraceae: Inuleae) detected by the segregation of genetic markers. *American Journal of Botany* 77: 1078–1083.

———, AND G. L. STEBBINS. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). *Systematic Botany* 12: 305–319.

CARDY, B. J., C. W. STUBER, AND M. M. GOODMAN. 1981. Techniques for starch gel electrophoresis of enzymes from maize (*Zea mays*

L.). Institute of Statistics Mimeograph series No. 1317. North Carolina State University, Raleigh, NC.

COATES, D. J. 1988. Genetic diversity and population genetic structure in the rare chittering grass wattel, *Acacia anomala* Court. *Australian Journal of Botany* 36: 273–286.

CRONQUIST, A. J. 1950. Notes on the Compositae of the northwestern United States. *Leaflets of Western Botany* 6: 41–56.

FLOWERS, T. J., M. A. HAJIBAGHERI, AND N. J. W. CLIPSON. 1986. Halophytes. *Quarterly Review of Biology* 61: 313–337.

GIGNAC, L. D., AND D. H. VITT. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. *Bryologist* 93: 7–22.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York, NY.

JOHN, E. A. 1989. An assessment of the role of biotic interactions and dynamic processes in the organization of species in a saxicolous lichen community. *Canadian Journal of Botany* 67: 2025–2037.

KARRON, J. D. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* 1: 47–58.

———, Y. B. LINHART, C. A. CHAULK, AND C. A. ROBERTSON. 1988. Genetic structure of populations of geographically restricted and widespread species of *Astragalus* (Fabaceae). *American Journal of Botany* 75: 1114–1119.

KUITTINEN, H., O. MUONA, K. KARKKAINEN, AND Z. BORZAN. 1991. Serbian spruce, a narrow endemic, contains much genetic variation. *Canadian Journal of Forest Research* 21: 363–367.

MARRIOTT, H. J. 1986. A report on the status of *Antennaria arcuata,* a candidate threatened species. Prepared for the U.S. Fish and Wildlife Service by the Wyoming Natural Diversity Database, The Nature Conservancy, Laramie, WY.

MCLAUGHLIN, S. 1986. Floristic analysis of the southwestern United States. *Great Basin Naturalist* 46: 46–65.

MEINZER, O. E. 1922. Map of the Pleistocene lakes of the basin-and-range province and its significance. *Bulletin of the Geological Society of America* 33: 541–552.

MORAN, G. F., O. MUONA, AND J. C. BELL. 1989. *Acacia mangium*: a tropical forest tree of the coastal lowlands with low genetic diversity. *Evolution* 43: 231–235.

NEI, M. 1972. Genetic distance between populations. *American Naturalist* 106: 283–292.

———. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences, USA* 70: 3321–3323.

NEVO, E., A. BEILES, AND T. KRUGMAN. 1988a. Natural selection of allozyme polymorphisms: a microgeographic climatic differentiation in wild emmer wheat (*Triticum dicoccoides*). *Theoretical and Applied Genetics* 75: 529–538.

———, ———, AND ———. 1988b. Natural selection of allozyme polymorphisms: a microgeographical differentiation by edaphic, topographical, and temporal factors in wild emmer wheat (*Triticum dicoccoides*). *Theoretical and Applied Genetics* 76: 737–752.

NICKRENT, D. L., AND D. WIENS. 1989. Genetic diversity in the rare California shrub *Dedeckera eurekensis* (Polygonaceae). *Systematic Botany* 14: 245–253.

NORUSIS, M. J. 1988. SPSS/PC+ V2.0 base manual for the IBM PC/XT/AT and PS/2. SPSS, Inc., Chicago, IL.

PLEASANTS, J. M., AND J. F. WENDEL. 1989. Genetic diversity in a clonal narrow endemic, *Erythronium propullens,* and in its progenitor, *Erythronium albidum. American Journal of Botany* 76: 1136–1151.

PORTER, S. C., K. L. PIERCE, AND T. D. HAMILTON. 1989. Late Wisconsinan mountain glaciation in the western United States. *In* H. E. Wright [ed.], Late-Quaternary environments of the United States, 71–111. University of Minnesota Press, Minneapolis, MN.

RICHMOND, G. M. 1986. Stratigraphy and correlation of glacial deposits of the Rocky Mountains, the Colorado Plateau and the ranges of the Great Basin. *In* V. Sibrava, D. Q. Bowen, and G. M. Richmond [eds.], Quaternary glaciations in the Northern Hemisphere, 99–127. Permagon Press, Toronto, ON.

ROHLF, F. J. 1987. NTSYS-pc: numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles). Applied Biostatistics, Inc., Setauket, NY.

ROSENFELD, I., AND O. A. BEATH. 1964. Selenium: geobotany, biochemistry, toxicity, and nutrition. Academic Press, New York, NY.

SMITH, G. R. 1978. Biogeography of intermountain fishes. *Great Basin Naturalist Memoirs* 2: 17–42.

SOLTIS, D. E., C. H. HAUFLER, D. C. DARROW, AND G. H. GASTONY. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *American Fern Journal* 73: 9–27.

TER BRAAK, C. 1985. CANOCO—a FORTRAN program for canonical correspondence analysis and detrended correspondence analysis. IWIS-TNO; Wageningen, The Netherlands.

———. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.

———. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69–77.

———. 1988. CANOCO—an extension of DECORANA to analyze species-environment relationships. *Vegetatio* 75: 159–160.

THOMPSON, R. S. 1988. Western North America: vegetation dynamics in the western United States: modes of response to climatic fluctuations. *In* B. Huntley and T. Webb [eds.], Vegetation history, 415–458. Kluwer Academic, Amsterdam.

———, AND J. I. MEAD. 1982. Late quaternary environments and biogeography in the Great Basin. *Quaternary Research* 17: 39–55.

VAN TREUREN, R., R. BIJLSMA, W. VAN DELDEN, AND N. J. OUBORG. 1991. The significance of genetic erosion in the process of extinction. I. Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. *Heredity* 66: 181–189.

VAN VALEN, L. 1965. Morphological variation and width of the ecological niche. *American Naturalist* 108: 377–390.

WEBER, W. A. 1987. Colorado flora: western slope. Colorado Associated University Press, Boulder, CO.

WELSH, S. A., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 1987. A Utah flora. *Great Basin Naturalist Memoirs* 9: 1–894.

WENDEL, J. F., AND N. F. WEEDEN. 1989. Visualization and interpretation of plant isozymes. *In* D. E. Soltis and P. S. Soltis [eds.], Isozymes in plant biology, 5–45. Dioscorides Press, Portland, OR.

WHITKUS, R. 1988. Modified version of GENESTAT: a program for computing genetic statistics from allelic frequency data. *Plant Genetics Newsletter* 4: 10.